Compensatory Growth and Mortality of the Hard Clam, *Mercenaria mercenaria* (Linnaeus, 1758)[1]

BY

PETER J. ELDRIDGE

Charleston Laboratory, National Marine Fisheries Service, P. O. Box 12607, Charleston, South Carolina 29412

AND

ARNOLD G. EVERSOLE

Department of Entomology, Fisheries & Wildlife, Clemson University, Clemson, South Carolina 29631

INTRODUCTION

The phenomenon of compensatory growth in fish populations has been described by many authors including Hodgson (1929), Ford (1933), Hubbs & Cooper (1934), Hile (1941), Scott (1949), Gerking (1966) and Ricker (1969, 1975). Growth compensation has been defined as the tendency for smaller fish of an age-group to catch up with larger ones [Sund, (1911) *in* Ricker (1969)]. Ricker (1975) more formally defined the phenomenon "as a correlation between increments in size in successive years of life among fish of a given year-class" and stated that "negative correlations indicate growth compensation, because they show that smaller fish tend to catch up with larger."

This phenomenon appears to be widespread in fish species and has been attributed at least in part to variation in time of spawning, water temperature during fry period, and differences in food availability for schools of fry (Sund, 1911). Gerking (1966) in his extensive study of bluegill growth proposed a mechanism for growth compensation. He suggested that within an age class smaller fish start growth earlier than their larger companions, thereby gaining a time advantage, assuming that the growing seasons of both end at the same time.

Overcrowding in nature as in the laboratory has been reported to inhibit growth and/or lower fecundity in molluscs (Chernin & Michelson 1957a, 1957b; Eisenberg, 1966; Berrie, 1968; Mooij-Vogelaar, Jager & van der Steen, 1970, 1973; Eversole, 1974; Peterson, 1978; Eldridge, Eversole & Whetstone, 1979; and others). Only Berrie (*op. cit.*) cited an example where molluscs exhibiting density-related growth inhibition experienced rapid growth when the density of snails per volumetric unit of pond was decreased by substantial collecting and heavy rainfall. Berrie's observation of rapid shell growth is unique. The lack of information concerning compensatory growth in molluscs may have been due, in part, to the difficulty in aging molluscs.

Eldridge *et al.* (1979) reported that growth rate of hard clams (*Mercenaria mercenaria* (Linnaeus, 1758) was significantly reduced by increased population density. The purpose of this study was to determine if three-year old clams that had experienced significantly reduced growth due to crowding could compensate with increased growth at a lower density. A second objective was to obtain an estimate of natural mortality for clams.

MATERIALS AND METHODS

Clams (mean = 13.0 mm shell length) obtained from Coastal Zone Resources Corporation of North Carolina in May 1975 were planted in protected trays containing approximately 14 cm of natural sediment. The clams, 5 months old at planting, were grown for 3 years (May 1975 - May 1978) at densities of 290, 869 and 1 159 clams/m^2 in a subtidal and in an intertidal location 15 m apart. The intertidal site was approximately 0.3 m above mean low water while the subtidal site was approximately 0.5 m below mean low water. Details concerning tray dimensions, tray density maintenance procedures, and location of planting site near Clark Sound, South Carolina are given in Eldridge *et al.* (1979).

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In May 1978, 2400 clams were selected randomly from the above 10000 clams held for the previous 3 years in the two tidal locations at 3 population densities. Each of 12 protected trays was planted with 200 clams (stocking density of 290 clams/m^2). Clams were planted according to their previous history. For example, 6 trays were planted at the intertidal site with clams that had been raised intertidally. Two trays contained clams from the previous density of 290 clams/m^2; two more trays held clams that had formerly been held at 869/m^2; and the remaining two trays held clams formerly cultured at a density of 1 159/m^2. Six trays were planted at the subtidal site with clams raised subtidally using the same protocol. Clams raised at a density of 290/m^2 and replanted at that density were considered controls. Shell lengths (SL, anterio-posterior axis) of all clams were measured at replanting time and at succeeding 6-month intervals from May 1978 to May 1980. Clams that died during the experiment were not replaced.

The SL of clams at initial planting were determined to be normally distributed. Mean SL (May 1978) were compared with the "t" statistic to determine if initial size differences existed between individual trays. To detect compensatory growth, correlation coefficients were calculated for 6-month intervals using the variables of mean SL and change in SL of each tray.

RESULTS AND DISCUSSION

Results of "t" tests showed that clams raised at the same density were similar in mean SL between trays (replicates) and tidal locations at start of the experiment. However, the mean SL of clams formerly held at a density of 869/m^2 were significantly smaller ($P < 0.05$) than those at 290/m^2; and clams formerly held at 1 159/m^2 were significantly smaller ($P < 0.05$) than both of the lower densities. These significant differences in SL among density treatments persisted throughout the experiment.

Adjustments (compensation) to reduced population densities were observed in absolute and relative growth (Table 1). Increases in mean SL between May 1978 and May 1980 were directly proportional to original densities. Shell lengths of clams formerly held at 1 159/m^2 and 869/m^2 increased approximately 10 mm and 8.5 mm during the experiment compared to only 5 mm for clams maintained at 290/m^2 (Table 1).

Correlation coefficients for change in SL versus mean SL were negative for each 6-month interval (Table 2). According to Ricker's (1975) definition, this population of hard clams, 3-5 years in age, exhibited compensatory growth. Also, the results of the experiment indicated that growth adjustments were influenced by reductions in population density.

Table 1

Changes in mean shell length (SL, mm) of hard clams 3-5 years old between May 1978 and May 1980.

Original Density May 1975-1978 (Age 0-3)	Replanted Density May 1978-1980 (Age 3-5)	Tidal Location	May 1978 Initial Mean SL ± SD (Range)	May 1980 Final Mean SL ± SD (Range)	Change in SL (% Increase)	May 1980 Survivors of 400 Replanted Clams
290[1]	290	I[2]	56.62 ± 4.34 (43.5 - 67.9)	61.85 ± 5.04 (46.1 - 76.2)	5.23 (9.24)	311
290	290	S[2]	57.09 ± 4.39 (36.3 - 72.2)	61.86 ± 4.42 (47.1 - 73.2)	4.77 (8.36)	394
869	290	I	49.14 ± 4.96 (34.4 - 62.1)	58.86 ± 5.13 (43.7 - 72.3)	9.72 (19.78)	290
869	290	S	50.05 ± 5.27 (31.6 - 63.9)	57.41 ± 4.61 (38.0 - 69.7)	7.36 (14.70)	389
1,159	290	I	45.99 ± 5.19 (29.2 - 59.7)	56.66 ± 4.91 (44.4 - 73.4)	10.67 (23.20)	147[3]
1,159	290	S	46.23 ± 5.35 (31.9 - 64.6)	56.31 ± 4.53 (42.6 - 74.7)	10.08 (21.67)	380

[1] Clams/m^2

[2] I = intertidal, S = subtidal

[3] One tray with approximately 198 clams of the original 200/tray planted in May 1978 was lost in Hurricane David, September 1979.

Table 2

Correlation coefficients for change in shell length (SL) versus mean SL of hard clams 3-5 years old for six month intervals between May 1978 and May 1980.

Six month intervals	Correlation coefficients	Number of trays	Number of individuals
May-November 1978	−0.70	12	2 362
November-May 1979	−0.77	12	2 343
May-November 1979	−0.69	11[4]	1 922
November-May 1980	−0.25	11	1 911

[4]One tray with approximately 198 clams was lost in Hurricane David, September 1979.

The ability to compensate in growth should be considered in clam culture operations. Accounts of this phenomenon in the literature for other species, as well as our own experience in raising clams, suggest that additional studies of compensatory growth need to be done before we can understand fully the interactions between age, size, and growing seasons. In addition to population density, many other environmental factors may affect compensatory growth, but not all of these may be controllable in extensive culture operations. Hence, it is more advantageous to start work on those factors that can be easily controlled to maximize production.

Instantaneous Mortality Rate (Z)

Hurricane David which brushed the South Carolina coast in September 1979 caused substantial mortality to intertidal clams; however, clams in subtidal trays appeared unaffected by the storm. Thus, only subtidal clams were used to calculate the instantaneous mortality rate (Z) for the experimental period (see Ricker, 1975:9 for explanation of computations). The calculated value for (Z) was 0.0144, which is equivalent to an annual mortality rate of 1.43% (Ricker, 1975:336). This estimate should be considered as underestimate because clams were protected from predators. However, for this age group, it does suggest that mortality from sources other than predation is quite low. Further research will be necessary before more accurate estimates of natural mortality can be determined for wild populations of hard clams.

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